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A simple method to estimate harvest index in grain crops

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Abstract

Several methods have been proposed to simulate yield in crop simulation models. In this work, we present a simple method to estimate harvest index (HI) of grain crops based on fractional post-anthesis phase growth (f_G = fraction of biomass accumulation that occurred in the post-anthesis phase). We propose that HI increases in a linear or curvilinear fashion in response to f_G. The linear model has two parameters, the intercept (HI_o) and the slope (s). The curvilinear model was assumed to be monotonic: $HI = HI_x - (HI_x - HI_o) \cdot \exp(-k \cdot f_G)$; where HI_x is the asymptote, HI_o is the intercept and k is a constant modulating the rate of HI increase. The models were tested for barley (Pullman, WA and Uruguay), wheat (Pullman, WA) and sorghum (Australia). A positive relationship between HI and f_G was in general evident. For barley, the linear model appropriately represented the response of HI to f_G, with both HI_o and s in the vicinity of 0.3. For wheat HI_o and s were 0.34 and 0.21, respectively, but the curvilinear model yielded a slightly better fitting than the linear model. For sorghum, both linear and linear-plateau models fitted data reasonably well. It is shown that the models work well in crops source-limited or source-sink co-limited during grain filling, but in sink-limited conditions the magnitude of the limitation needs to be characterized to compute HI. A major advantage of this method is that the parameters of the linear or curvilinear model are readily calibrated from yield data and biomass measurements at anthesis and harvest.
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1. Introduction

Crop simulation models are widely used for the quantitative analysis of cropping systems, typically providing robust estimation of biomass production based on the availability, capture, and use-efficiency of solar radiation, water, and nitrogen. Simulating the fraction of the produced biomass that is allocated to grain constitutes, however, a greater challenge for these models. The methods used to simulate grain yield can be grouped in two general approaches: (1) simulating yield components (e.g. Villalobos et al., 1996), and (2) simulating the fraction of the total aboveground biomass allocated to the grain (harvest index, HI) (e.g. Williams et al., 1989; Stöckle et al., 1994).

The yield components approach is based on the empirical observation that growth during a critical window of time around anthesis is related to the number of grains per plant or per unit area (Fischer, 1985; Kiniry et al., 2002). Using this relationship, the number of grains generated for a given crop can be predicted based on simulated phenology and crop growth (e.g. Villalobos et al., 1996). To compute yield, the individual grain weight needs to be simulated. Cultivar-dependent features are accommodated by using empirical coefficients that need to be estimated for each genotype. Disadvantages of this method are that yield components are difficult to simulate due to compensation among components, the use of several yield components augments the opportunities for errors during the simulation, and it requires labor-intensive calibration.

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The simulation of HI has basically followed two approaches. One approach is to increase the HI from a given time after anthesis until physiological maturity or a maximum preset HI is reached (e.g. Williams et al., 1989). Hammer and Muchow (1994) and Hammer and Broad (2003) concluded that despite its simplicity, this method has limited applicability because it is difficult to assign a correct value to the HI increase rate and to the timing of the HI plateau onset, the latter usually occurring after two-thirds of the time between anthesis and physiological maturity (Hammer and Muchow, 1994). Another approach is to use functional relationships that estimate directly the final HI (Stöckle et al., 1994). Sadras and Connor (1991) proposed a functional relationship in which the HI is positively and asymptotically related to the fraction of water transpired after anthesis (f_T) (Passioura, 1997; Richards and Townley-Smith, 1987). To develop their model, it was assumed that the contribution of preanthesis assimilates to yield decreases linearly as f_T increases (Richards and Townley-Smith, 1987), biomass was corrected by the energetic cost of producing carbohydrate-, oil-, or protein-rich tissue, and transpiration was normalized by the vapor pressure deficit (Bierhuizen and Slatyer, 1965).

In this paper, we present two variants of a method to estimate HI that is conceptually based on that described by Sadras and Connor (1991). We propose that HI is related to the fractional post-anthesis phase growth (f_G). We discuss some theoretical implications and demonstrate the method applicability for simulating HI of wheat, barley, and sorghum.

2. Materials and methods

2.1. Model development

We propose that HI is related to f_G, the latter defined as the ratio between aboveground biomass produced post-anthesis and that produced from emergence to maturity. Similar to Sadras and Connor (1991), HI is computed at physiological maturity without providing the time evolution of grain growth. The simplest relationship is to assume that HI is a linear function of f_G with slope s or: $dHI/df_G = s$. Integration yields:

$$HI = HI_o + s \cdot f_G, \tag{1}$$

where the intercept HI_o represents HI when there is no change in biomass from anthesis to maturity ($f_G = 0$). By definition, in an absolute source-limited situation, all the reserves available at anthesis minus the respiration cost (expressed fractionally as HI_o) and all the biomass produced post-anthesis (expressed fractionally as f_G) are used for grain growth. Therefore, at a given f_G, there is a maximum attainable HI that we called potential HI (HI_P) and is a special case of Eq. (1):

$$HI_P = HI_o + (1 - HI_o) \cdot f_G, \tag{2}$$

where $1 - HI_o = s$. An example of HI_P is shown in Fig. 1 along with a computed proportional contribution of reserves to yield. When $f_G = 0$ all grain yield originates from the reserves available at anthesis. Hypothetically, when $f_G = 1$ (all growth occurred after anthesis) then $HI_P = 1$. As f_G increases the
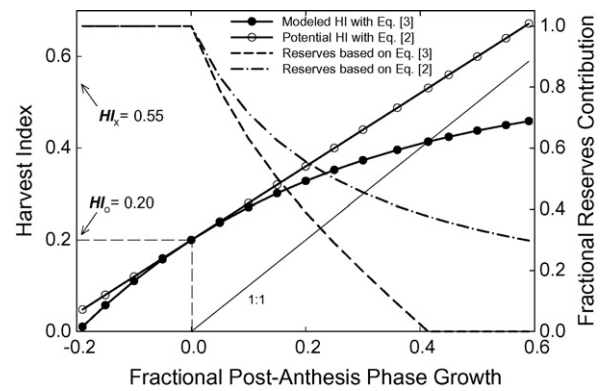

Fig. 1. Theoretical response of the harvest index (HI) to the fractional post-anthesis phase growth (f_G). The HI was computed using a linear response of HI to f_G equation (2) with $HI_o = 0.2$, and using a curvilinear response Eq. (3) with $HI_x = 0.55$, $HI_o = 0.20$, and $k = 2.3$. The fractional reserves contribution to yield was calculated based on the modeled HI with Eq. (2) (dashed-doted line) or Eq. (3) (dashed line).

relative contribution of reserves to yield decreases Fig. 1. A source-sink co-limitation situation can be defined as that in which HI increases as f_G increases, but the potential sources for grain filling are not fully utilized and therefore $0 < s < 1 - HI_o$.

Another approach is to assume that the relationship between HI and f_G is curvilinear. This assumption can be derived from the model proposed by Sadras and Connor (1991), in which as f_T increases, HI approaches a maximum (HI_x) asymptotically. Since transpiration and biomass production are closely related, we propose that f_T in their model is a surrogate for f_G. A relationship in which the rate of change of HI in response to f_G decreases as HI approaches HI_x is represented by $dHI/df_G = k \cdot (HI_x - HI)$, where k is a constant relating the rate of change of HI with respect to f_G. Integration from $f_G = 0$ ($HI = HI_o$) gives:

$$HI = HI_x - (HI_x - HI_o) \cdot \exp(-k \cdot f_G). \tag{3}$$

An example with Eq. (3) is shown in Fig. 1. The fractional contribution to yield of reserves accumulated before anthesis relates quasi-linearly to f_G (Fig. 1). At f_G greater than that obtained where the 1:1 line crosses the HI curve (Fig. 1), grain filling does not require reserves accumulated before anthesis and, in theory, the mass of organs other than grain should increase. Eq. (3) represents a source-sink co-limited situation because as f_G increases so does HI but reserves are increasingly unused.

To be physiologically meaningful, the HI computed with Eq. (3) should be less or equal than HI_P Eq. (2). This is achieved by setting the following constraint on k:

$$k \leq \frac{1 - HI_o}{HI_x - HI_o}. \tag{4}$$

In Fig. 1, where absolute source-limited and source-sink co-limited situations are plotted using the same HI_o and the constraint for k specified by Eq. (4), the degree of sink limitation is represented by the difference between the lines corresponding to Eqs. (2) and (3). Both Eqs. (1) and (3)

accommodate an eventual decrease in biomass from flowering to maturity due to reserves consumption by respiration. In such case, the carbon balance for the crop is negative while transpiration is positive.

Reserves accumulation and use in cereals is not restricted to pre-anthesis reserves. In barley and wheat the maximum accumulation of reserves in stems occurs in the post-anthesis phase, roughly in the first third of the linear phase of grain growth (Austin et al., 1977; Borrel et al., 1989; Snyder et al., 1993). Therefore, part of the biomass produced after anthesis that is translocated to the grain could have been transiently stored, a dynamic element not considered in the method proposed. Nevertheless, considering Eq. (1), for two genotypes with identical HI_o, differences in s can be interpreted as differences in reserves use for grain growth. Similar considerations apply for HI_o, HI_x and k in Eq. (3).

As described here, these models, as well as that of Sadras and Connor (1991), do not take into account absolute sink-limited conditions, i.e. when the sum of post-anthesis growth and pre-anthesis accumulated reserves exceed the biomass needed to fill the grains to their potential weight. A sharp decrease in grain setting due to stress at anthesis represents an extreme case of sink-limitation; the HI will be relatively low due to the grain number reduction. Ignoring the sink-limitation would cause an overestimation of HI. A crop growing unstressed after anthesis might face a similar situation for relatively high f_G (i.e. high availability of assimilates per grain). Both Eqs. (1) or (3) would be valid at explaining the variation in HI with f_G up to the point in which further increase in f_G will not cause an increase in HI but conceivably a stabilization or a decrease in HI, because the sink potential size has been reached. For Eq. (1), this can be accommodated by a linear-plateau model, while in Eq. (3) the asymptotic response of HI to f_G will likely imply minor errors in HI estimation. Eventually, the parameters of Eqs. (1) and (2) can also be a function of the degree of sink limitation. We extend the analysis of this point when presenting data on barley, wheat, and sorghum.

Whether the linear or the curvilinear approach represent appropriately the response of HI to f_G needs to be tested empirically, a task that we pursue for three crops in this paper. The parameterization of either of these approaches requires only accurate biomass measurements at flowering and maturity, and grain yield. The biomass energetic content of seed and non-seed tissue can be adjusted to a common basis for oil- or protein-rich seed crops. A brief description of the experimental information used, summarized in Table 1, follows.

2.2. Field data

Data from several experiments were assembled for spring barley, spring wheat and sorghum. The main criterion for experiment selection was availability of accurate information on biomass at anthesis and at maturity, and grain yield. In addition, experiments in barley and wheat were conducted where we attempted to manipulate f_G and HI by clipping the crop to the ground at the four- to five-leaves stage (details in Table 1). Clipping annual grasses at that stage promotes tillering, changes

the plants habit from erectile to prostrate, and increases the HI relative to intact plants (O. Ernst, personal communication).

Spring barley data on HI and f_G collected in six different experiments, three in Pullman, WA, and three in Uruguay, were grouped and used to calibrate the parameters s, HI_x, HI_o, and k for barley. In Pullman, the sample area ranged from 0.1 to 0.5 m^2 at anthesis and was 2 m^2 at maturity. In the experiment in Uruguay data was obtained for individual stems. The sampling procedure in the three experiments was identical. At anthesis of each plot, 200 spikes at the same phenological stage were labeled with plastic red rings. Ten stems per plot were randomly sampled twice a week from anthesis until well after physiological maturity. Dry weight of each stem was recorded, the spikes threshed while recording the number of grains per spike, and the dry weight recorded. Sterile florets in each spike were detected (lateral florets ignored), counted, and weighted separately. The ratio between sterile florets (excluding lateral florets) and the total number of florets (spikelets) per spike was calculated and is referred hereafter as sterility. The HI for each individual stem was calculated, and the final HI of each plot was estimated fitting a segmented model to HI versus time (t): $HI = a$ [for $t < t_{lag}$] + a + $b(t - t_{lag})$ [for $t_{end} < t < t_{lag}$] + a + $b(t_{end} - t_{lag})$ [for $t \geq t_{lag}$], where t_{lag} is the initial lag period in which HI remains constant at its initial value a, b is the slope of HI increase, and t_{end} is the time at which HI stabilizes.

Spring wheat data on HI and f_G collected over five years from different experiments near Pullman, WA, were grouped and used to calibrate the parameters s, HI_x, HI_o, and k and to test the model(s) (Table 1). Details on the experiments conducted between 1987 and 1989 (Exp 7–9) are given in Huggins (1991); only treatments with accurate estimations of anthesis are included (fertilization rates >90 kg N ha^{-1}). Biomass samples were taken at anthesis and physiological maturity and f_G estimated from the dry weights. Samples at anthesis consisted of 10 plants randomly selected within each plot. Aboveground biomass per unit area was estimated as the product of the average plant weight and density. At physiological maturity, 1-m long samples from a center row were used to calculate HI. Grain yield was obtained by harvesting four (1987 and 1988) or five (1989) center rows of each plot (1.2 m × 6.0 m) with a plot combine.

Aboveground biomass at maturity was estimated by dividing the plot yield by the HI. For Exp 10–12 (Pullman, WA) samples at anthesis and maturity were 0.5 and 2 m^2, respectively. The samples were threshed and the HI and f_G estimated from the dry weights. The model parameters generated for spring wheat were tested on the winter wheat cultivar Falcon (Exp 13). This experiment was identical to Exp 10 except for the cultivar used. All statistical analyses were performed with SAS (SAS Institute, 1999); the standard error is reported along with treatment averages and parameter estimates.

Data on f_G and HI for sorghum was obtained from the literature. The criteria for selecting data were that: (1) phenology was accurately documented; and (2) crops did not experience water stress at anthesis. All information for sorghum came from experiments conducted in Australia. Data from Muchow (1989) were obtained in Katherine, Northern Territory

Table 1
Summary of the experimental information used to calibrate the model for barley and wheat

Experiment	Location	Sources of variation	Comments
Spring barley			
Exp 1	Pullman, WA 46°45′N, 117°12′W elevation 756 m	Two years (2000–2001); two seeding dates (April and June); two cultivars (Baronesse and Steptoe); two densities (100 and 200 plants m^{-2})	No-till seeded, irrigated experiment; soil Palouse (Pachic-Ultic Haploxerol); Details in Kemanian et al. (2004)
Exp 2	Pullman, WA 46°47′N, 117°5′W elevation 773–815 m	Year 2002; seven plots located along a SW-NE transect covering a gradient of soils and stored soil water	Dryland experiment fertilized with 146 kg N ha^{-1} and 22 kg P ha^{-1} Cultivar Baronesse; soils Palouse (Pachic-Ultic Haploxerol)-Thatuna (Oxyaquic Agrixerolls)-Naff (Typic Argixerolls)
Exp 3	Pullman, WA 46°47′N, 117°5′W elevation 773–815 m	Year 2004; four blocks located along a SW-NE transect; two treatments: intact and clipped crops at the four- to five-leaves stage	Dryland experiment fertilized with 123 kg N ha^{-1} and 11 kg P ha^{-1} Cultivar Baronesse; soils Palouse (Pachic-Ultic Haploxerol)-Thatuna (Oxyaquic Agrixerolls)-Naff (Typic Argixerolls)
Exp 4	Sayago, Uruguay 34°49′S, 56°13′W elevation 54 m	Year 1996; six cultivars (Aphrodite, Bowman, Clipper, FNC6-1, MN599, Estanzuela Quebracho)	Fertilization: 100 kg N ha^{-1} Soil Typic Argiudol (FAO classification)
Exp 5	Paysandú, Uruguay 32°19′S, 58°04′W elevation 55 m	Idem Exp 4	Idem Exp 4
Exp 6	Paysandú, Uruguay 32°19′S, 58°04′W elevation 55 m	Year 1997; six cultivars (Aphrodite, Bowman, Clipper, Dephra, FNC6-1, Estanzuela Quebracho); two seeding dates (May and July); two clipping treatments (intact and clipped)	Fertilization: 60 kg N ha^{-1}; clipping treatment applied 15 days after five-leaf target stage in May seeding date
Spring wheat			
Exp 7	Whitman Co, WA 46°58′N, 117°28′W	Year 1987; tillage (no-till and moldboard plow-based tillage); four nitrogen fertilization rates, and sulfur fertilization rates (not reported in this paper)	Cultivar WB926R; details in Huggins (1991)
Exp 8	Whitman Co, WA 46°68′N, 117°18′W	Year 1988; preceding crop (Austrian winter pea or winter wheat); tillage (light harrowing before seeding or not); six nitrogen fertilization rates.	Cultivar WB926R; details in Huggins (1991)
Exp 9	Whitman Co, WA 46°68′N, 117°23′W	Year 1989; tillage (no-till and moldboard plow-based tillage); five nitrogen fertilization rates.	Cultivar WB926R; details in Huggins (1991)
Exp 10	Pullman, WA 46°47′N, 117°5′W elevation 773–815 m	Year 2001; irrigation (dryland and 50 mm of irrigation after anthesis)	Cultivar Hank; crop fertilized with 155 kg N ha^{-1}
Exp 11	Pullman, WA 46°47′N, 117°5′W elevation 773–815 m	Year 2002; seven plots located along a SW-NE transect covering a gradient of soils and stored soil water	Cultivar Hank; crop fertilized with 155 kg N ha^{-1}
Exp 12	Pullman, WA 46°47′N, 117°5′W elevation 773–815 m	Year 2004; preceding crop spring barley and spring peas; clipping (intact and clipped at four-leaves stage)	Cultivar Hank; crop fertilized with 155 kg N ha^{-1}
Winter wheat			
Exp 13	Pullman, WA 46°47′N, 117°5′W elevation 773–815 m	Year 2002; irrigation (dryland and 50 mm of irrigation after anthesis)	Cultivar Falcon

Details of the experiments are given in Section 2.

(14°28′S, 132°18′E, elevation 108 m), for one hybrid (Dekalb DK55) planted in three seeding dates. Data for the same hybrid grown at two fertilizer levels (0 and 240 kg N ha^{-1}) at Gatton, south-eastern Queensland (27°33′S, 152°20′E, elevation 90 m) were obtained from Muchow and Sinclair (1994). Data from Kamoshita et al. (1998) were obtained in Gatton, Queensland for 16 grain sorghum hybrids grown under three fertilization levels (0, 60, and 240 kg N ha^{-1}).

3. Results

3.1. Spring barley

Data of Exp 1–3 were used to calibrate the parameters of both Eqs. (1) and (3) for spring barley (Fig. 2). The data cover a range of f_G (HI) from 0.3 (0.4) to 0.7 (0.6). In these experiments the water supply by irrigation, precipitation and stored water prevented the occurrence of water stress at anthesis, and sterility was not observed. The clipping treatment of Exp 3 increased the HI with respect to the control (0.48 versus 0.46, $n = 5$, $P < .01$); however when graphed with the data of Exp 1 and 3, data from the clipped treatment did not depart from the general trend (Fig. 2).

The relationship between HI and f_G was linear in the range provided, and indicate a sink-source co-limited response as the slope s obtained was less than $1 - HI_o$ (Table 2). The fitting was not improved by Eq. (3). Therefore, Eq. (1) seems to appropriately represent the response of HI to f_G in spring barley for this experimental data.
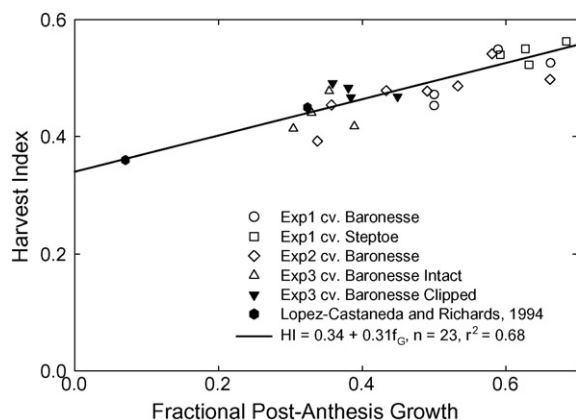
Fig. 2. Harvest index (HI) as a function of the fractional post-anthesis phase growth (f_G) for two cultivars of spring barley (Baronesse and Steptoe) in Pullman, WA (details of the experiments in the text). The average of four cultivars and two locations in Australia (López-Castañeda and Richards, 1994a) is also shown but was not included in the fitting. The fitted equation is shown extrapolating the data range to illustrate the expected HI response.

In contrast with the experiments in Pullman, the experiments in Uruguay exposed the crops in some cases to excess precipitation that saturated the soils temporarily, resulting in sterility levels of up to 57% for one cultivar (Table 3). This data set provided an opportunity to quantify the impact of sink limitation on HI. Examples of the computation of the final HI using a segmented model are shown in Fig. 3. As expected, there was variability in the rate of increase of *HI*, in particular among experiments. The rates of increase of HI were between 0.01 and 0.02 d^{-1}, similar to those reported in wheat (Wheeler et al., 1996) and sorghum (Hammer and Broad, 2003). The linear segmented model provided accurate estimates of both the final HI and the duration of the HI increase (Fig. 3).

Table 3
Fractional post-anthesis growth (f_G), harvest index (*HI*) and spike sterility in the experiments with spring barley conducted in Uruguay

Experiment[a]	Seeding date	Treatment	f_G	*HI*	Sterility
Exp 4			0.39	0.45	0.12
Exp 5			0.47	0.53	0.00
Exp 6	1st	Intact	0.40	0.46	0.25
		Clipped	0.35	0.44	0.25
	2nd	Intact	0.41	0.48	0.12
		Clipped	0.45	0.48	0.23

The values are averages across cultivars.

[a] Exp 4 experienced temporary flooding in the week pre-anthesis due to 100 mm precipitation; Exp 5 experienced severe water stress pre-anthesis that was relieved at anthesis by timely precipitation; Exp 6 suffered excess precipitation during the entire crop cycle and in addition, the clipping treatment was applied two weeks late affecting growth and yield negatively.

Data from Exp 4–6 are from individual stems, mostly main stems, and thus the results are not directly comparable with those of Exp 1–3. Maximum observed HI for plot data in Uruguay are <0.50, while computed values based on single stems were up to 0.58 (Fig. 3). Fitting Eq. (1) to these data yielded $HI_o = 0.29 \pm 0.08$, $s = 0.41 \pm 0.20$ ($n = 30$, $r^2 = 0.13$, $P < 0.05$), a rather poor result (Fig. 4) that we surmise was the result of sterility (Table 3). Including sterility as another regression variable in Eq. (1), showed that HI decreased in quadratic fashion in response to sterility independently of f_G (Fig. 4, Table 2). Therefore, in this case the effect of sink limitation on HI could be easily accounted for because sterility was known. For example, for sterility = 0.3, the HI was $0.3^2 = 0.09$ points lower than that obtained with sterility = 0. It can also be shown that HI was almost unaffected by sterility <0.15, which implies yield compensation through grain weight. With the effect of sterility removed, the slopes

Table 2
Fitted parameters ($\pm$S.E.) of the linear equation (1) and curvilinear model equation (3) representing the response of harvest index (*HI*) to fractional post-anthesis growth (f_G)

Source[a]	Linear				Curvilinear				
	HI_o	s	$HI_{plateau}$	r^2	HI_o	HI_x	k	r^2	n
Barley									
Exp 1–3	0.34 ± 0.02	0.31 ± 0.04	–	0.68^{***}	0.33 ± 0.12	1.5 ± 10.3	0.3 ± 3.2	0.68^{***}	23
Exp 4–6[b]	0.38 ± 0.04	0.30 ± 0.09	–	0.84^{***}	–	–	–	–	30
Wheat									
Exp 7–12	0.34 ± 0.01	0.21 ± 0.04	–	0.37^{***}	0.31 ± 0.05	0.52 ± 0.15	2.0 ± 2.7	0.39^{*}	46
Ref1	0.30 ± 0.04	0.35 ± 0.14	–	0.31^{*}	–	–	–	–	15
Ref2	0.26 ± 0.02	0.64 ± 0.004	–	0.92^{***}	–	–	–	–	15
Sorghum									
Ref3	0.20 ± 0.02	0.50 ± 0.04	–	0.89^{***}	0.15 ± 0.03	0.80 ± 0.00	1.3 ± 0.1	0.82^{***}	18
	–	–	–	–					18
DK55	0.14 ± 0.04	0.66 ± 0.12	–	0.76^{**}	–	–	–	–	12
DK55[c]	0.07 ± 0.05	0.90 ± 0.16	0.47 ± 0.02	0.83^{**}	–	–	–	–	12

[*], [**], and [***] significant at the 0.05, 0.01, and 0.001 probability level, respectively.
[a] Exp 1–3 and Exp 7–12 from Pullman, WA; Exp 4–6 from Paysandú and Sayago, Uruguay; Ref1 (Regan et al., 1992) and Ref2 (van Herwaarden et al., 1998) from Australia; Ref3 (Kamoshita et al., 1998) from Australia, only six hybrids considered here, fitting the curvilinear model respecting the constraint imposed on k by Eq. (4) was feasible only by setting $HI_x \geq 0.80$ (see text for explanation); data for DK55 was obtained in Australia and reported in Muchow (1989), Muchow and Sinclair (1994), and Kamoshita et al. (1998).
[b] The full model includes a quadratic response to sterility (v^2), with the quadratic coefficient of the response = -1.01 ± 0.09.
[c] The sum of squares reduction test comparing the linear and the linear-plateau model for DK55 was significant at $P < 0.08$.
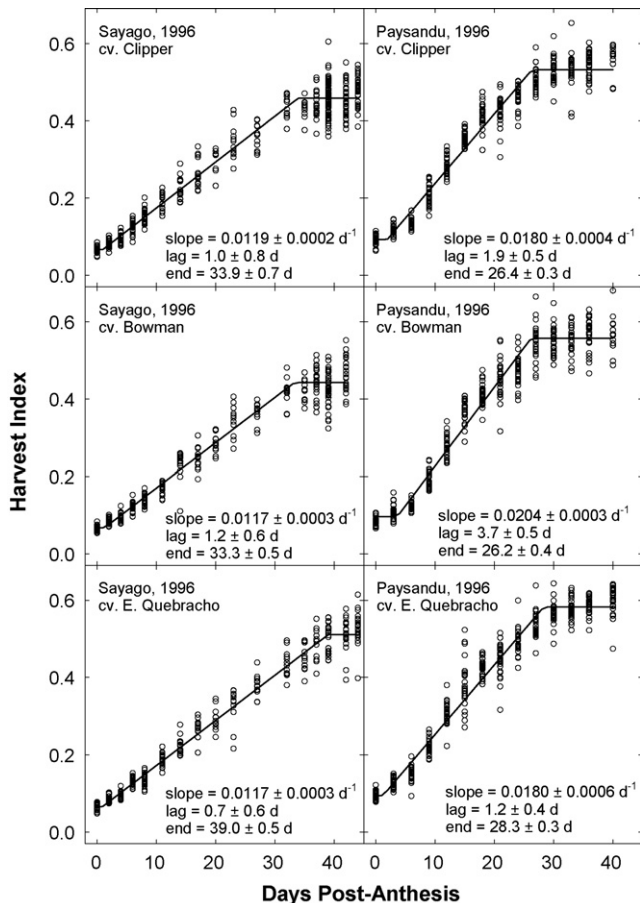
Fig. 3. Harvest index (HI) increase during grain filling in three cultivars of spring barley (Clipper, E. Quebracho, and Bowman) in two sites (Sayago and Paysandú, Uruguay) in the year 1996. Each point represents an individual stem. The first sample corresponds to anthesis, where HI represents the weight of lemma and palea divided by the total stem weight. A segmented linear model was fitted to the data, and estimates of the beginning of the linear increase in HI (lag ± S.E.), end of HI increase (end), and slope are reported. The standard errors are optimistic estimates because they were obtained from linear regression without considering the time series correlation between measurements and ignoring the apparent gamma distribution of the residuals.

obtained in these experiments (Exp 4–6) and in Pullman (Exp 1–3) are identical (~0.3, Table 2), reinforcing the validity of Eq. (1) at representing the response of HI to f_G in spring barley. The intercept is considerably higher in Exp 4–6 (0.38 versus 0.33), likely reflecting the difference between plot and individual stem data.

3.2. Spring wheat

In Exp 7–12 a variety of treatments were applied and their effect on f_G and HI is briefly summarized before presenting the parameters fitted to Eq. (1) and (3). For Exp 7–9, the within-year treatments had almost no effect on either HI or f_G, but the three years depict a clear trend of increasing HI as f_G increases (Fig. 5). On average, HI (f_G) were 0.46 (0.42), 0.38 (0.17), and 0.41 (0.28) for the years 1987, 1988, and 1989, respectively. In 2001 (Exp 10, cv. Hank), irrigation increased both HI (0.44 ± 0.01 versus 0.42 ± 0.01) and f_G (0.47 ± 0.03 versus
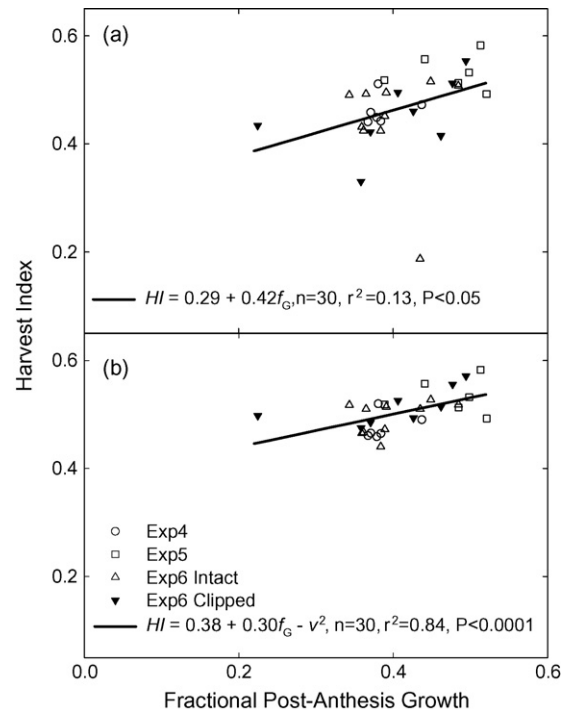

Fig. 4. Harvest index (HI) as a function of the fractional post-anthesis phase growth (f_G) for seven spring barley cultivars in Uruguay (details of the experiments in the text). Panel (a) shows the raw data and fitting of a linear model, and panel (b) shows the data corrected by the square of the observed sterility, as indicated in the regression equation and explained in the text. The slope of the regression obtained after correcting for sterility is identical to that of spring barley in Pullman, WA (Fig. 2).

0.41 ± 0.04) (Fig. 5). In 2004 (Exp 12) the clipping treatment increased HI (0.42 ± 0.02 versus 0.39 ± 0.02) and f_G (0.36 ± 0.04 versus 0.31 ± 0.05).

Fitting the parameters for the linear and curvilinear models for the cultivars WB926R and Hank together yielded reasonable responses of HI to f_G (Table 2). The fitting for Eq. (1) was slightly better than that of Eq. (3) and is shown in Fig. 5. There is variability in the data as highlighted by the coefficient of determination and the large standard error of k (Table 2). The fitted k is below the maximum k estimated with Eq. (4), indicating that reserves remobilization are limited in these cultivars or in this environment. Given the variability of treatments that originated the data shown in Fig. 5, the fitted equation represents the response of HI to f_G reasonably well. An independent database to test this model for these spring wheat cultivars is not available.

However, we have data for winter wheat from Exp 13 from the same location. The testing shows that the model predicted the HI for both dryland and irrigated crops well (RMSE = 0.014, MAD = 0.013, $n = 10$), even though the parameters were fitted for spring wheat (Fig. 5).

3.3. Sorghum

Kamoshita et al. (1988) presented a comprehensive data set for both f_G and HI of sorghum. The treatments included
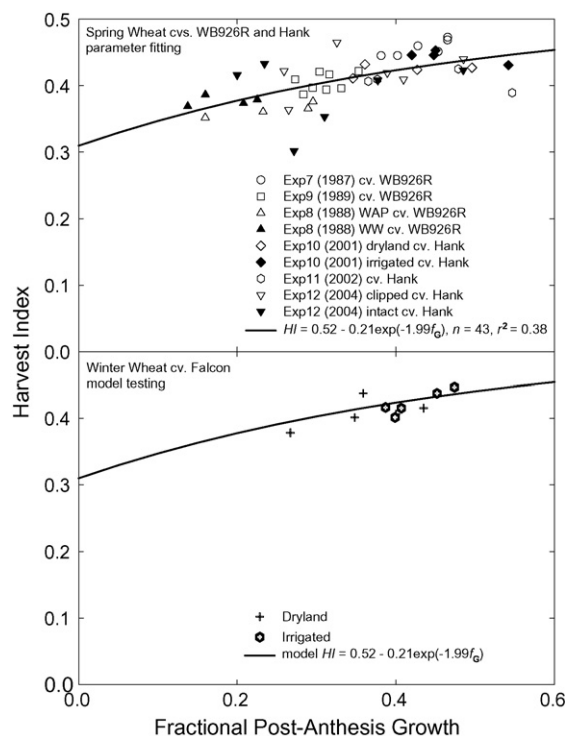
Fig. 5. Harvest index (HI) as a function of the fractional post-anthesis phase growth (f_G) for two cultivars of spring wheat (WR926R and Hank) in six experiments in Pullman, WA (upper panel) and a testing of the same model in data for winter wheat cv. Falcon (lower panel). Details of the experiments are given in the text. The fitted equation is shown beyond the data range to show the expected extrapolated HI response.

nitrogen fertilizer rates and 16 hybrids. The range of f_G obtained, however, was limited, with basically all $f_G > 0.30$ (Fig. 6). On average, increasing fertilization from 0 to 240 kg N ha^{-1} increased total biomass at maturity, yield, and HI (Table 2 of Kamoshita et al., 1998).

The response of the HI to f_G depended on the hybrid. By visually inspecting the data, we separated the hybrids' responses into three groups: (1) no response of HI in the range of f_G obtained (three hybrids), (2) linear response (seven hybrids), and (3) curvilinear or linear-plateau response (six hybrids) (Fig. 6). The three hybrids that showed no response of HI to f_G are by definition sink-limited. The yield of these hybrids was in general lower than the total post-anthesis growth (all data points to the right of the 1:1 line). Seven hybrids showed a linear response of HI to f_G, but we cannot assess if the response can get "saturated" as in case (3) at increasing f_G levels.

For the hybrids showing a linear response (only six of the seven hybrids considered, the hybrid DK 55 is analyzed separately below), a linear regression yielded $HI_o = 0.20$ and $s = 0.50$ (Table 2, Fig. 6b). Fitting Eq. (3) respecting the constraint imposed on k by Eq. (4) was feasible only by setting $HI_x \geq 0.80$ (Table 2).

A group of six hybrids showed a seemingly curvilinear or linear-plateau response of HI to f_G (Fig. 6c). We cannot discriminate between these two models because of lack of data. Assuming that the linear-plateau response is correct, visual inspection suggests that the hybrids differ in the f_G at which they reach the HI plateau value (Fig. 6c). All but one hybrid seem to have $s = 1$ for $f_G < 0.5$ and complete dependence on post-anthesis phase growth for HI to increase, indicating a source-limited condition up to that threshold. Kiniry et al. (1992) reported that the reserves stored previous to grain filling have little impact on yield for sorghum hybrids grown in central Texas, which seems to be the situation of these hybrids.

The data of the hybrid Dekalb DK55 presented by Muchow (1989) and Muchow and Sinclair (1994) were combined with data for the same hybrid from Kamoshita et al. (1998) and are presented in Fig. 7. We fitted both a linear and a linear-plateau model (Table 2). A sum of squares reduction test indicated that the linear-plateau was better than the linear model ($P < 0.08$), yielding also better residuals distribution. The threshold f_G calculated was 0.45 ± 0.04; up to $f_G = 0.45$, the response is almost identical to Eq. (2) (HI_p). Fitting Eq. (3) was not possible for this data set. Overall, the response of this hybrid seems to be intermediate between those hybrids showing a linear response
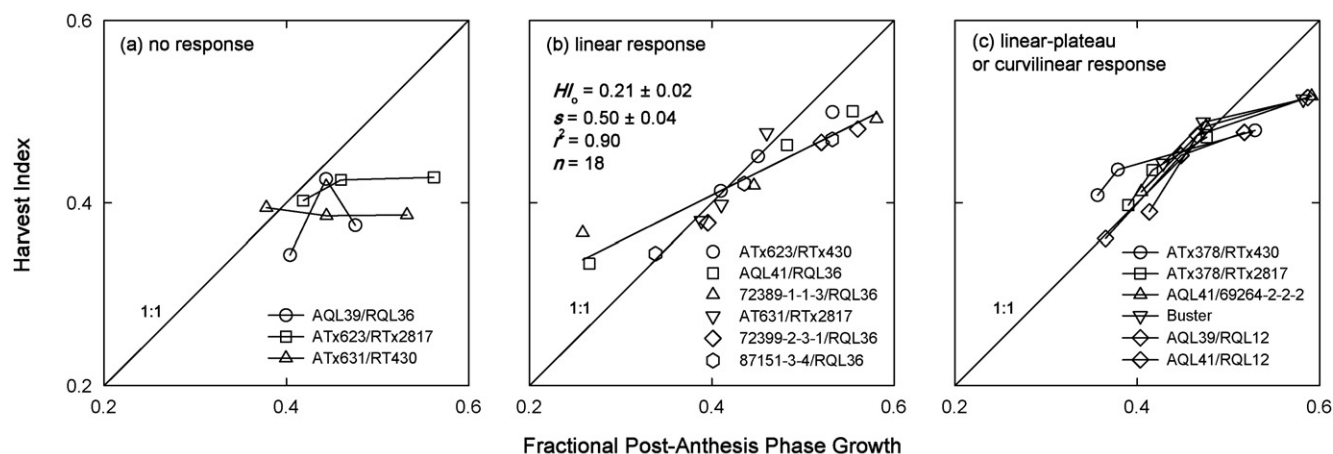

Fig. 6. Harvest index (HI) as a function of the fractional post-anthesis phase growth (f_G) of 15 grain sorghum hybrids. The hybrids were separated into three groups: hybrids showing no response of HI to f_G (left panel), hybrids showing a linear response (middle panel, intercept = HI_o, slope = s), and hybrids showing a linear-plateau response. Variations in HI and f_G originated from nitrogen fertilization rates. Original data from Kamoshita et al. (1998).
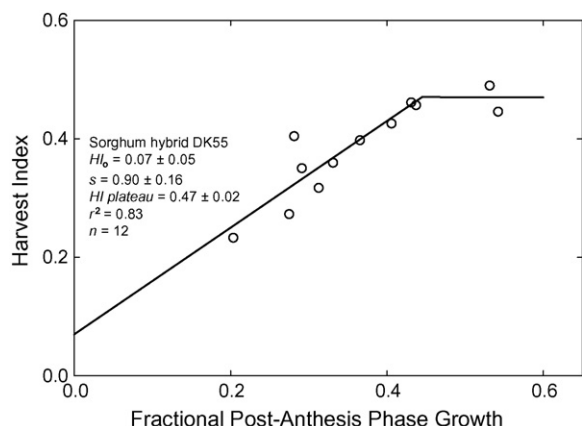
Fig. 7. Harvest index (HI) as a function of the fractional post-anthesis growth (f_G) for the grain sorghum hybrid DK55. Variability in HI and f_G originated from different seeding dates (Muchow, 1989), and from nitrogen fertilization rates (Muchow and Sinclair, 1994; Kamoshita et al., 1998). The fitted equation is shown beyond the data range to show the expected extrapolated HI response.

and some dependence on reserves (HI$_o \sim 0.20$) and those with a linear-plateau response and no dependence on reserves.

4. Discussion

The response of HI to f_G proposed is consistent with several lines of evidence. Sinebo (2002) found a correlation between HI (range 0.19–0.38) and the fractional duration of the post-anthesis phase in barley. Similarly, López-Castañeda and Richards (1994a) found in a Mediterranean environment a negative correlation between HI and days to anthesis in barley, wheat, triticale, and oats. Earlier flowering in that environment allows grain filling to occur before both temperature and the vapor pressure deficit increase, conceivably increasing f_G. Data for spring barley from López-Castañeda and Richards (1994a,b) obtained under acute water stress after anthesis is well represented by the model fitted for spring barley in Pullman, WA (Fig. 2). Siddique et al. (1989), also working in a Mediterranean environment, found that higher yield in modern wheat cultivars in comparison to old cultivars was associated with earlier flowering. Accordingly, the HI and f_G were higher for modern (post-1975 releases) than for old (pre-1975 release) cultivars (0.36 versus 0.30 for HI, and 0.23 versus 0.19 for f_G, respectively). Hammer and Muchow (2003) presented data for two hybrids with contrasting time for maturity: S34 (short cycle) and RS671 (longer cycle) but with similar average yields. The hybrid with shorter cycle had on average higher f_G (0.54 versus 0.41) and higher HI (0.53 versus 0.47) than that with the longer cycle.

Regan et al. (1992) presented data for several wheat genotypes grown in Wongan Hills (Australia), and van Herwardeen et al. (1992) reported data for three localities and different nitrogen fertilizer rates in Australia. In both cases we found that HI correlated positively with f_G ($r = 0.56$, $n = 15$, $P < 0.05$ for Regan et al., 1992; and $r = 0.96$, $n = 15$, $P < 0.001$ for van Herwardeen et al., 1992). The intercepts compared well with those reported for small grains in Pullman, WA (Table 2).

The slopes, while always representing source-sink co-limited situations, show more variation.

The form of the dependence of HI on f_G is not unique and likely reflects differences in the balance between yield components determined by the genotype or environmental conditions. The analysis for sorghum suggests that depending on the genotype, the response is linear, linear-plateau, or curvilinear. The parameter HI$_o$ seems to converge for both barley and wheat around 0.3. López-Castañeda and Richards (1994a) reported that, in an experiment with low f_G (ca. 0.05), the HI of barley, wheat, durum wheat, and triticale ranged from 0.3 to 0.35. van Herwaarden et al. (1998) reported that the apparent re-translocation of pre-anthesis biomass to grain was around 25% for spring wheat. The parameters HI$_o$, s, HI$_x$, and k are plausibly genotype- and environment-dependent; in the data analyzed, HI$_o$ was narrowly bounded in wheat and barley (ca. 0.3), and showed more variability in sorghum (range 0–0.2).

Since the functionality of this approach relies on accurately defining anthesis, it will probably work better for determinate crops in which anthesis concentrates in a narrow time window. Crops with an extended flowering period overlapping grain filling, like soybean or cereals seeded at low density, might be poorly handled. While this method yields HI at harvest, it could be used to provide an upper, moving boundary of HI during grain filling, to the HI increase method used by Hammer and Muchow (1994). For each time step, f_G and a boundary value of HI can be computed by using either Eq. (1) or (3). Grain growth will continue provided the HI does not exceed that moving boundary, which will vary as the season progresses and f_G increases, or the crop reaches physiological maturity.

5. Conclusions

The proposed dependence of HI on f_G provides a simple, easy to parameterize, and conceptually sound framework to analyze variations in HI and to estimate HI in crop simulation models. The method is good for source-limited and source-sink co-limited situations.

Acknowledgments

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